

REVIEW OF NORTH AMERICAN PACIFIC COAST BEACH VEGETATION

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The objective of this paper is to summarize, mainly through a review of the literature, beach vegetation and its phytogeography along the Pacific Coast of North America between Point Barrow, Alaska (approximately 71°N), and Cabo San Lucas, at the southern tip of Baja California (approximately 23°N, fig. 1). "Beach" is that strip of sandy land from just above mean high water to just beyond the reach of storm waves, or, if there is a foredune, to the top of the foredune. The term "strand" has often been applied to this strip of land, but it is clear from a number of floras that the concept of strand varies widely: it may apply to the very edge of shore only, or to the beach plus adjacent inland dunes, even though most dune species do not extend onto the beach. To avoid ambiguity, we have chosen the more intuitive term beach. As defined here, the beach habitat is characterized by a maritime climate, high exposure to air-borne salts and sand blast, and a shifting substrate with a low water-holding capacity and low organic matter content.

The survey of beach vegetation does not include species of adjacent habitats such as dunes, ocean-facing cliffs, salt marshes, shingle beaches, and the intertidal unless those species are also characteristic of beach vegetation. Exclusion of dune species is justified in an ecological sense, for levels of both soil- and air-borne salinity drop appreciably behind the beach (Barbour et al., 1973; Boyce, 1954; Martin and Clements, 1939; Oosting and Billings, 1942). Plants of dunes may be xerophytes, but they are not obligate halophytes (Barbour, 1970b; Martin and Clements, 1939; Purer, 1934, 1936). Kearney (1904) first raised the question of whether beach plants are halophytes, but data accumulated since then (see review by Barbour, 1970d) indicate that levels of salt spray are high, even if soil salinity levels are not. Beach plants are either facultative halophytes or salt-tolerant glycophytes.

Exclusion of cliff species, although necessary, is regrettable. On windy, rocky, open coasts, plants of ocean-facing cliffs receive considerable amounts of salt spray, enough spray to cause some authors to call them "quite salt tolerant" (Calder and Taylor, 1968) or "strongly halophytic" (Peck, 1961). However, the more stable substrate that typically consists of a developed soil with greater water holding capacity distinguishes the bluff habitat from the more xeric, sand blasted beach. Furthermore, the number of species found in this habitat is quite high, and slight changes in aspect or in access to fresh water permits normally inland species to

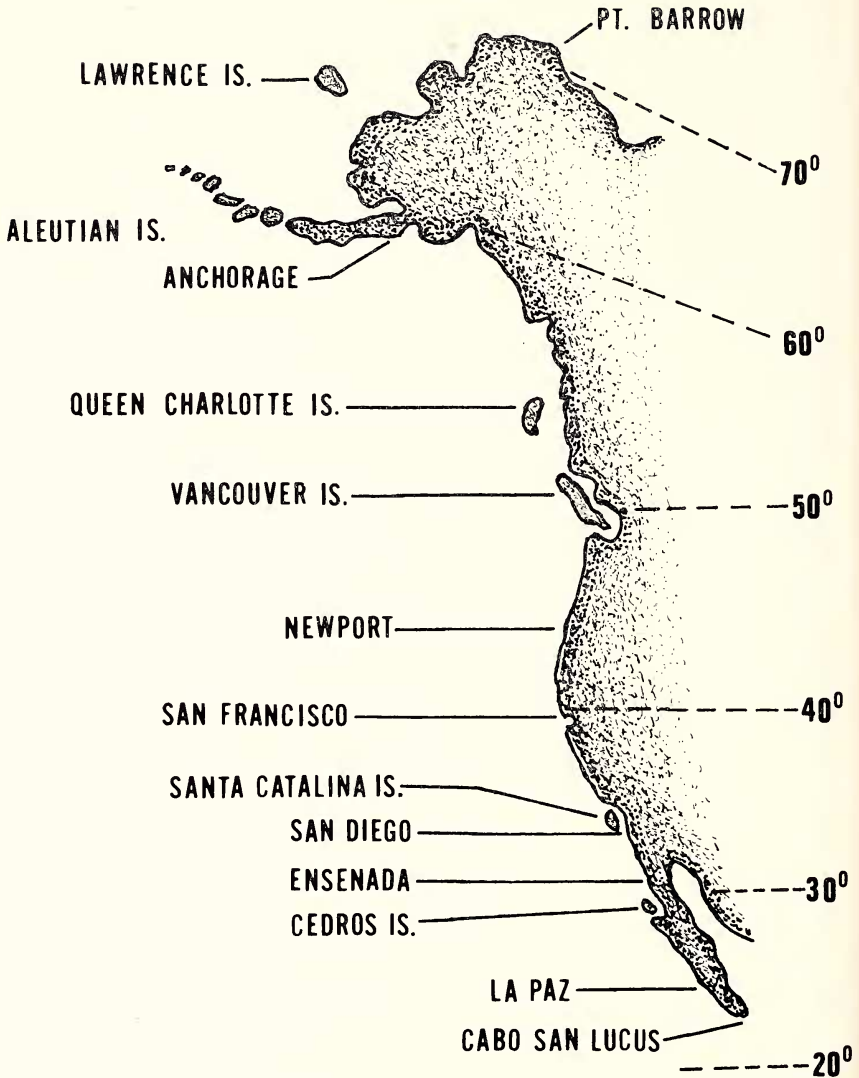


FIG. 1. The Pacific coast of North America.

occur almost side-by-side with more strictly halophytic species. Given only the information presented in the average flora, it is quite difficult to decide which species are the halophytes. At Bodega Head, California, for example, ocean-facing cliffs support truly restricted species such as *Artemisia pycnocephala*, *Eriophyllum staechadifolium*, *Armeria maritima* var. *californica*, *Jaumea carnosa*, and *Plantago maritima*, but, if a seep runs down the bank, then typically grassland species such as *Anagallis*

arvensis, *Polypogon monspeliensis*, and *Sonchus asper* follow (Barbour, 1970a).

Shingle beaches are excluded, because their substrate stability is greater than that of sandy beaches. The flora of shingle beaches is more closely related to that of salt marshes than to sandy beaches.

Throughout this paper we are concerned with those vascular plants that most characterize beach vegetation. The distribution limits that we present are for taxa where they occur on the beach. In several cases species extend further north or south than our limits, but not in the beach habitat. Furthermore, we have approximated latitudinal limits to the nearest half degree because many isolated beaches along the coast have not been botanized, especially in British Columbia and Baja California.

Much ecological work also remains to be done. Chapman (1964) states that the strand ". . . has not been subjected to serious study . . ." and very little is known about the requirements of the individual species, or even about the nature of the environment". Few synecological and autecological studies of beach vegetation have been published. Apparently the only experimental work done on a Pacific coast beach plant is by Barbour (1970b, 1970c, and 1972b) and Barbour and Rodman (1970) on *Cakile maritima* and *C. edentula* spp. *californica*—which regrettably are not even native to the Pacific coast. They were introduced to the San Francisco area during the past 90 years and have spread rapidly north to Alaska and south to Baja California. Barbour concluded that *Cakile maritima* shows no ecotypic variation in germination, growth, or flowering along the Pacific Coast, but extrapolating from *Cakile* to other beach plants may be a tenuous procedure.

It is striking that several introduced species have spread so far and contribute so significantly to vegetation: *Mesembryanthemum edule*, two *Cakile* species, and *Ammophila arenaria*. Why are they able to do so well on the Pacific coast? Are there more unoccupied niches (if such things do really exist) on this coast than on others? Will further introductions be able to do as well or is the habitat space now filled? In this connection it may be ominous to recall a statement by Calder and Taylor (1968) that *Lolium perenne* has been introduced to beaches in the Queen Charlotte Islands for the purpose of erosion control. Already, at Sandspit, it ". . . is now one of the dominant grasses in this region". It appears that the South American Pacific Coast may similarly be open to invasion. Kohler (1970) points out that *Ambrosia chamissonis* and *Lupinus arboreus* have been introduced to Chile from North America, yet today they dominate beach and dune vegetation.

Cooper (1936, 1958, 1967) has recounted in detail where and when marram grass (*Ammophila arenaria*) was introduced to the Pacific Coast from Europe, and how rapidly it seems to be spreading naturally, producing in many places a foredune where none existed before. Marram

grass may “. . . in the course of decades or centuries change significantly the character of the whole dune complex”. Apparently, a foredune was not present along the central portion of the coast until *Ammophila* was introduced. We have unpublished data from Pt. Reyes, California, that further show species diversity is depressed by *Ammophila*; *Elymus*-dominated foredunes exhibit twice as many species as adjacent *Ammophila*-dominated foredunes.

The fact that few ecological studies of beach vegetation have been conducted is unfortunate, because beach vegetation may prove to be an exceptionally good “validation site” for hypotheses generated in studies of other vegetation types, where competition confounds the picture. MacArthur (1972), has hypothesized that the warm limit of any species' range is most often determined by competition, not by climate. What happens on the strand? MacArthur (1972) and Axelrod and Bailey (1969) have independently postulated that species diversity is affected more by temperature equability than by seasonal uniformity of precipitation. We can test this along the beach, for it includes areas with both equable temperature and moisture (Washington), areas with only temperature equability (Northern California), and areas with neither temperature nor moisture equability (Southern California and Baja California). Unfortunately, considering the increasing human population and rate of destruction of beaches along some parts of the coast, beach vegetation may be a disappearing type. Judging from reviews of Oosting (1954) and Ranwell (1972), ecological studies of beach species are a bit more numerous for Japan, Great Britain, and the east coast of the United States.

SOURCE MATERIAL

Most of the information summarized in this section comes from floras. We wish to document our choice of references in some detail because they had such a strong bearing on our ultimate choice of beach species. Most of the floras lumped beach with dune or other coastal habitats, and only by elaborate cross-checking and personal observations could we determine which species listed in fact extended onto the beach. Cooper's fine survey of Pacific Coast strand and dune flora (1936) serves as an initial, central reference. Information about Alaskan and Baja Californian floras, however, was quite limited at that time, and therefore his survey was incomplete. His approach was not ecological, but his notes on distribution do permit one to distinguish beach species from dune species.

More recent information for the north portion of the coast can be obtained from Wiggins and Thomas' flora of the Alaskan Arctic Slope (1962), Hultén's flora of the Aleutian Islands (1937) and his flora of Alaska (1968), which includes areas south of Vancouver Island, Young's flora of St. Lawrence Island (1971), and Calder and Taylor's flora of the Queen Charlotte Islands (1968). Of the four, Calder and Taylor's

flora contains the most detailed community descriptions and habitat notes, and the Alaskan flora contains the least (but it has the best information on overall species' distributions). References to relative abundance, coupled with photographs of habitats in the texts, lead to some conclusions as to which species were most characteristic of the beach. A recent synecological paper for Amchitka Island (Amundsen and Clebsch, 1971), though short, is very helpful.

For the central portion of the coast, we utilized major reviews by Schofield (1969) and Franklin and Dyrness (1973), Jones' survey of the Olympic Peninsula (1936), Peck's Oregon flora (1961), Kumlér's study of succession on Oregon dunes (1969), Munz's California flora (1973), Barbour's extensive floristic and ecological data for Bodega Head, California (Barbour, 1970a-d, 1972a, 1972b; Barbour and Rodman, 1970; Barbour et al., 1973), Howell's Marin County flora (1970), Thomas' Santa Cruz flora (1961), Hoover's San Luis Obispo County flora (1970), an ecological survey of Morro Bay State Park by Williams (1974) and Williams and Potter (1972), Smith's brief flora of the Santa Barbara region (1952), and the autecological studies of Martin and Clements at Santa Barbara (1939). The overview of Pacific Coast vegetation by Knapp (1965) was so brief as to be only marginally useful.

For southern California and all of Baja California, we used Boughey's checklist of Orange County plants (1968), Thorne's flora of Santa Catalina Island (1967), the lay-oriented booklet on prominent plants of coastal San Diego County by Higgins (1956), and Shreve and Wiggins' classic work on the Sonoran desert (1964). Information on Baja California was especially difficult to find, and likely sources such as Nelson's major reference work on the natural resources of Baja California (1922) and the reports of many miscellaneous botanizing expeditions (e.g., Brandegee, 1889; Johnson, 1958; and Orcutt, 1885), were very disappointing in their omission of beach plants. We have relied heavily on an M.S. thesis by Ann Johnson (1973) and on personal communications from Dr. Ira Wiggins.

A number of other floras were examined, but these did not add new material beyond that found in the above references, so they will not be cited here. Some of our floristic and climatic material also appears in a review by Macdonald and Barbour (1974), but we have considerably refined their summary. In addition the following treatments were consulted for determining species' distributions outside of the area considered and for determining possible affinities of the endemic beach species: Bowden, 1957; Fernald and Weatherby, 1916; Hall and Clements, 1923; Hermann, 1960; Lewis and Oliver, 1965; Payne, 1964; Payne et al., 1973; Raven, 1969; Rodman, 1974; St. John, 1970; Small, 1895; Swallen, 1944; and Tillett, 1967.

Nomenclature in general follows Hulten (1968) for the northern portion of the coast, Munz (1968) for the central portion, and Shreve and Wiggins (1964) for the southernmost portion. The excellent five

volume flora of the Pacific Northwest by Hitchcock et al. (1969) was particularly useful because of its full treatment of nomenclatural synonyms and for its discussions of species' affinities.

CLIMATE

The Pacific Coast of North America sweeps in a broad diagonal across 48° of latitude and 55° longitude and extends from Arctic tundra to the sub-tropical southern fringe of the Sonoran Desert (fig. 1). Climatic variations are considerable, yet because the warm North Pacific Current bathes the shores of the Aleutians, southern Alaska, and British Columbia, and the cold California Current bathes the southern coastline, the change in climate is not as extreme as experienced inland over shorter distances.

Climatic parameters for selected Pacific Coast stations are shown in Table 1. We have used the unmodified Koeppen system as described by Trewartha (1954) and have not used minor changes in it suggested by Ackerman (1941). We selected only weather stations on the coast at sea level.

The maritime climate shows increasing temperature equability southward to Point Reyes, California (38°N), where it is maximum and then begins to decrease again southward. Annual precipitation, although more irregular in its pattern, shows a similar southward increase—maximizing between $59^\circ30'$ and 57°N on the Alaskan mainland and then decreasing gradually southward. Minimum annual precipitation occurs at Bahia Magdalena, Baja California ($20^\circ40'$), where it is 1/40 of that at Yakutat, Alaska. South of Bahia Magdalena annual rainfall again begins to increase. It is possible to pinpoint six major shifts of climate.

1) At about 60°N , between Anchorage and Yakutat, Alaska, climate shifts from Df (microthermal) to Cfb (mesothermal), due to warming in the winter months; in addition, precipitation increases ninefold, as one moves south from Anchorage to Yakutat.

2) At 46°N , Seaside, Oregon, Cfb shifts to Csb; that is, a Mediterranean pattern of rainfall begins here and continues south. Winter temperatures continue to rise. Summer fog is common from here south through Baja California.

3) At 37°N , between Santa Cruz and Monterey, California, Cs (mesothermal) changes to BEs (semi-arid), due to declining precipitation. Temperatures do not change markedly.

4) At about 31°N , between Ensenada and El Socorro, Baja California, BS (semi-arid) shifts to BW (arid). Again, temperatures do not markedly change, but rainfall decreases.

5) At about 29°N , between El Rosario and Punta Abreojos, Baja California, BWk shifts to BWH due to mean yearly temperatures rising above 18°C . There are not enough stations in the 3° span between El Rosario and Punta Abreojos to be very sure about the dividing line.

TABLE 1. CLIMATIC DATA FOR SELECTED STATIONS ALONG THE PACIFIC COAST. Sources: Armstrong (1971), Arias (1942), Calder and Taylor (1968), Climate of British Columbia (1944), Climatological data (1968), Eber et al. (1968), Hambidge (1941), Hastings and Humphrey (1969), Koepfen (1931), Trewartha (1954), Wiggins and Thomas (1962), and Young (1971).

No.	Station name	Latitude (N)	Annual ppt. (mm)	Number of frost-free days/year	Mean air temperature (°C)			Mean water temperature (°C)		
					Year	Coldest mo.	Warmest mo.	Coldest mo.	Warmest mo.	Koepfen category
1	Pt. Barrow, Alas.	71°20'	103	8	-12	9	0	8	ET	
2	Kotzebue, Alas.	66°50'	200		-6	11			Df/ET	
3	Nome, Alas.	64°30'	468	73	-3	10			Df/ET	
4	Gambell, St. Lawrence Is., Alas.	64°00'	504		-5	7			ET	
5	Anchorage, Alas.	61°20'	358	118	1	14	4	13	Df	
6	Yakutat, Alas.	59°30'	3350		3	12			Cfb	
7	Sitka, Alas.	57°00'	3300	157	6	13			Cfb	
8	Sandspit, Queen Charlotte Is., Br. Co.	53°15'	1253	207	6	14	7	15	Cfb	
9	Amchitka, Alas.	51°30'	828		4	9	2	9	ET	
10	Clayoquot, Victoria Is., Br. Co.	49°10'	2675	230	9	15	8	15	Cfb	
11	Tatoosh Is., Wash.	48°25'	1950	322	9	13	6	13	Cfb	
12	Aberdeen, Wash.	47°00'	2147	197	10	16	4	16	Cfb	
13	Seaside, Ore.	46°00'	1085	251	11	16	6	16	Cf (barely)	
14	Newport, Ore.	44°35'	1555	248	10	7	14	15	Csb	
15	Eureka, Cal.	40°45'	970	328	11	14	11	13	Csb	
16	San Francisco, Cal.	37°45'	505	356	12	14	10	13	Csbn	
17	Santa Cruz, Cal.	37°00'	710(!)	351(1)	14	17	11	13	Csbn	
18	Monterey, Cal.	36°40'	460	364	13	17	10	17	BSskn	
19	Morro Bay, Cal.	35°20'	426	320	14	18	13	16	BSskn	
20	Santa Catalina, Cal.	33°22'	334	365	16	19	14	17	BSskn	
21	San Diego, Cal.	32°40'	250	365	17	22	13	17	BSskn	
22	Ensenada, B. C.	31°50'	245	365	17	21	13	14	BSskn	
23	El Socorro, B. C.	30°20'	110	365	17	21	13	19	BWskn	
24	El Rosario, B. C.	30°00'	83	365	17	22	16	22	BWskn	
25	Punta Abreojos, B. C.	26°45'	103	365	21	28	17	28	BWshn	
26	Bahia Magdalena, B. C.	24°40'	81	365	21	27	18	27	BWwh	
27	Todos Santos, B. C.	23°25'	179	365	22	28	18	28	BWwh	
28	Cabo San Lucas, B. C.	22°50'	250	365	24	29	20	28	Aw	

6) At about 23°30'N, near Todos Santos, BWs (arid, summer dry) shifts to Aw (tropical, winter dry). Winter and summer temperatures rise and so does precipitation.

The possible significance of these six points to phytogeography will be discussed in a later section of this paper.

PHYTOGEOGRAPHY

Distribution Types. It should be emphasized that we are treating only characteristic beach taxa and have not attempted to assemble an exhaustive beach flora. Thus we are dealing with ecological, rather than truly floristic units.

Our review indicates that there are some 46 species that characterize beaches of the Pacific Coast of North America. These have been arranged sequentially in Table 2 by their northern range limit.

The beach taxa, at the species level, can be divided into nine distribution types (fig. 2). Table 2 lists specific and subspecific taxa, but we have found it simpler and no less precise to deal only at the species level. As circumscribed, the categories are used both to define geographic affinities of the beach flora and to distinguish possible migratory routes. I. Circumarctic: 5 species, 11 percent of the flora.

Taxa: *Festuca rubra*, *Honckenya peploides*, *Lathyrus japonicus*, *Ligusticum scoticum*, *Mertensia maritima*.

Species in this group have either circumarctic or widespread arctic distributions. The latter two species occur in both North America and Eurasia but are absent along the arctic coasts of either Siberia or Canada or both. Disruption in these otherwise circumpolar ranges can be attributed to lack of summer warmth or destructive action of pack ice (Young, 1971).

II. Beringian-Eastern North America: 5 species, 11 percent of the flora.

Taxa: *Angelica lucida*, *Conioselinum chinense*, *Elymus mollis*, *Poa eminens*, *Senecio pseudo-arnica*.

Species included here range across Beringia and extend both north and south along the Pacific Coast. Disjunct populations also occur on the Atlantic Coast of North America and in some species additional populations are found on the Great Lakes and Hudson Bay. The disjunct distributions of these species tend to support the supposition that many of the Beringian species formerly occupied greater areas in the arctic (Young, 1971).

III. Beringian: 2 species, 4 percent of the flora.

Taxa: *Carex macrocephala*, *Glehnia littoralis*.

IV. Maritime-Endemic: 13 species, 28 percent of the flora.

Taxa: *Abronia latifolia*, *A. maritima*, *Agrostis pallens*, *Ambrosia chamissonis*, *Camissonia cheiranthifolia*, *Chamaesyce leucophylla*, *Jouvia pilosa*, *Lathyrus littoralis*, *Poa douglasii*, *Polygonum paronychia*, *Suaeda californica*, *Tanacetum douglasii*, *T. camphoratum*.

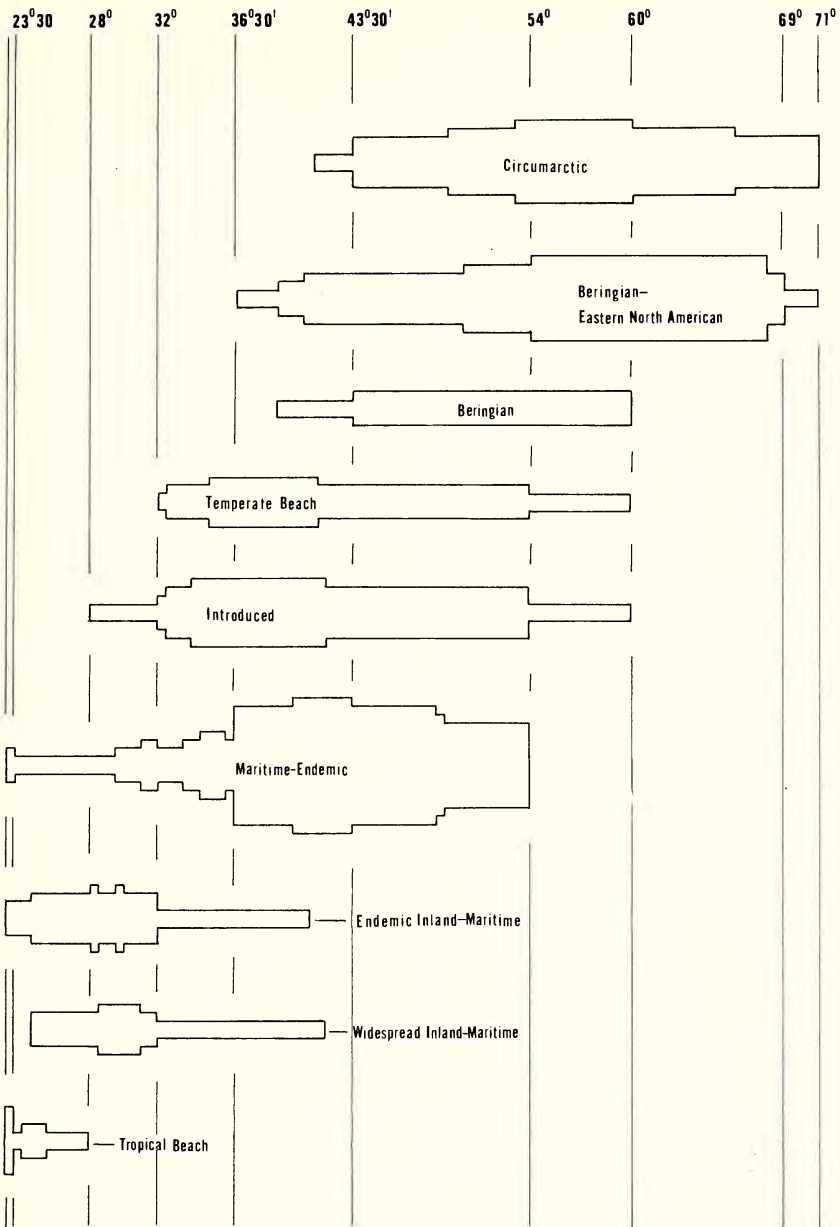


FIG. 2. Latitudinal distribution of the nine species-distribution types, from 23°30' to 71° N latitude. Width of the bars is proportional to number of species.

TABLE 2. LATITUDINAL RANGES AND DISTRIBUTION PATTERNS FOR THE CHARACTERISTIC BEACH SPECIES OF THE NORTH AMERICAN PACIFIC COAST. Latitudinal limits are to the nearest 30'. The ranges given are only for the North American Pacific Coast and only for the species as an element in the beach vegetation. Range extensions due to occurrence in non-beach habitats are given in parentheses. The numbers of the right column refer to the zone or subzone in which the taxon occurs. (1a, Arctic; 1b, Near Arctic; 2, Subarctic; 3a, Temperate North Coastal; 3b, Temperate Mediterranean; 4, Dry Mediterranean; 5, Northern Arid; 6, Southern Arid; 7, Tropical.)

Species and Distribution Pattern	Limits, N. lat.		Total Range	Zones or subzones of occurrence
	North	South		
<i>Elymus mollis</i> Trin., Beringian-E.N.A.	71°	36° 30'	34° 30'	1a,1b,2,3a,3b
<i>Lathyrus japonicus</i> Willd., Circumarctic	71°	41°	30°	1a,1b,2,3a,3b
ssp. <i>japonicus</i> , Circumarctic	71°	41°	30°	1a,1b,2,3a,3b
ssp. <i>pubescens</i> (Hartm.) C. Regel, Circumarctic	71°	52° 30'	18° 30'	1a,1b,2,3a
<i>Honckenya peploides</i> (L.) Ehrh., Circumarctic				
ssp. <i>peploides</i> , Circumarctic	71°	63° 30'	7° 30'	1a,1b
ssp. <i>major</i> (Hook.) Hult., Beringian	65°	43° 30'	21° 30'	1b,2,3a
<i>Mertensia maritima</i> (L.) S.F. Gray, Circumarctic	71°	53°	18°	1a,1b,2,3a
<i>Senecio pseudo-arnica</i> Less., Beringian-E.N.A.	69°	50°	19°	1b,2,3a
<i>Poa eminens</i> Presl, Beringian-E.N.A.	69°	54°	15°	1b,2
<i>Conioselinum chinense</i> (L.) BSP., Beringian-E.N.A.	68°	39°	29°	1b,2,3a,3b
<i>Angelica lucida</i> Spreng., Beringian-E.N.A.	68°	40° 30'	27° 30'	1b,2,3a,3b
<i>Ligusticum scoticum</i> L., Circumarctic				
ssp. <i>hultenii</i> (Fern.) Calder & Taylor, Beringian	66°	49°	17°	1b,2,3a
<i>Cakile edentula</i> (Bigel.) Hook., Temperate Strand, E.N.A.				
ssp. <i>californica</i> (Heller) Hult., Introduced	60°	32° 30'	27° 30'	2,3a,3b,4
<i>Fragaria chiloensis</i> (L.) Duchn., Temperate Strand				
ssp. <i>pacifica</i> Staudt., Temperate Strand	60°	35°	25°	2,3a,3b,4
<i>Glehnia littoralis</i> F. Schm., Beringian				
ssp. <i>leiocarpa</i> (Math.) Hult., Maritime Endemic	60°	39°	21°	2,3a,3b
<i>Carex macrocephala</i> Willd., Beringian	60°	43° 30'	16° 30'	2,3a
<i>Festuca rubra</i> L., Circumarctic				
ssp. <i>acuta</i> (Krecz. & Bobr.) Hult., Beringian	60°	43° 30'	16° 30'	2,3a
<i>Cakile maritima</i> Scop., Introduced	54°	28°	26°	3a,3b,4,5
<i>Ambrosia chamissonis</i> (Less.) Greene, Maritime Endemic	54°	31°	19°	3a,3b,4,5
ssp. <i>cuneifolia</i> (Nutt.) Payne, Maritime Endemic	50°	46°	4°	3a
<i>Calystegia soldanella</i> (L.) R. Brown, Temperate Strand	54°	32°	22°	3a,3b,4
<i>Ammophila arenaria</i> (L.) Link, Introduced	54°	34°	20°	3a,3b,4

TABLE 2. *Continued.*

Species and Distribution Pattern	Limits, N. lat.		Total Range	Zones or subzones of occurrence
	North	South		
<i>Abronia latifolia</i> Eschs., Maritime Endemic	54°	34°30'	19°30'	3a,3b,4
<i>Lathyrus littoralis</i> (Nutt. ex T. & G.) Endl., Maritime Endemic	54°	36°30'	17°30'	3a,3b
<i>Poa douglasii</i> Nees, Maritime Endemic	54°	36°30'	17°30'	3a,3b
ssp. <i>macrantha</i> (Vasey) Keck.	54°	39°	15°	3a,3b
ssp. <i>douglasii</i>	41°30'	36°30'	5°	3b
<i>Agrostis pallens</i> Trin., Maritime Endemic	54°	37°30'	16°30'	3a,3b
<i>Tanacetum douglasii</i> DC., Maritime Endemic	49°	40°	9°	3a,3b
<i>Polygonum paronychia</i> C. & S., Maritime Endemic	48°30'	36°30'	12°	3a,3b
<i>Camissonia cheiranthifolia</i> (Hornem. ex Spreng.) Raim., Maritime Endemic	43°30'	33°30'	10°	3b,4
ssp. <i>cheiranthifolia</i>	43°30'	34°30'	9°	3b,4
ssp. <i>suffruticosa</i> (S. Wats.) Raven	34°30'	33°30'	1°	4
<i>Heliotropium curassavicum</i> L., Widespread Inland-Maritime				
ssp. <i>oculatum</i> (Hiller) Jtn., Widespread Inland-Maritime	42°	24°30'	17°30'	3b,4,5,6
<i>Mesembryanthemum edule</i> L., Introduced	42°	32°	10°	3b,4
<i>Mesembryanthemum chilense</i> Mol., Temperate Strand?	41°30'	32°30'	9°	3b,4
<i>Atriplex leucophylla</i> (Mcq.) D. Dietr., Inland-Maritime Endemic	41°	28°	13°	3b,4,5
<i>Tanacetum camphoratum</i> Less., Maritime Endemic	37°30'	36°30'	1°	3b
<i>Abronia maritima</i> Nutt. ex Wats., Maritime Endemic	36°	24°	12°	4,5,6
<i>Lycium brevipes</i> Benth., Inland-Maritime Endemic	32°	23°15'	10°45'	5,6,7
<i>Distichlis spicata</i> (L.) Greene, Widespread Inland-Maritime	32° (50°)	28°30' (23°15')	3°30' (26°45')	5
<i>Salicornia subterminale</i> Parish, Inland-Maritime Endemic	32°	29°30'	2°30'	5
<i>Suaeda californica</i> S. Wats., Maritime Endemic	32°	29°30'	2°30'	5,6
<i>Allenrolfea occidentalis</i> (S. Wats.) Kuntze, Widespread Inland Maritime	31°	24°30'	6°30'	5,6
<i>Frankenia palmeri</i> S. Wats., Inland-Maritime Endemic	30°	27°	3°	5,6
<i>Astragalus magdalenae</i> Greene, Inland-Maritime Endemic	28°30' (33°)	24°30' (23°15')	4°	5,6
<i>Sesuvium verrucosum</i> Raf., Tropical Strand	28°	24°	4°	6
<i>Atriplex barclayana</i> (Benth.) Dietr., Inland-Maritime Endemic	27° (32°)	23°15'	3°45'	6,7
<i>Sporobolus virginicus</i> (L.) Kunth, Tropical Strand	25°30'	23°15'	2°15'	6,7
<i>Chamaesyce leucophylla</i> (Benth.) Millsp., Maritime Endemic	24° (24°30')	23°15'	45'	7

TABLE 2. *Continued.*

Species and Distribution Pattern	Limits, N. lat.		Total Range	Zones or subzones of occurrence
	North	South		
<i>Jouvea pilosa</i> (Presl.) Scribn., Maritime Endemic	23°30'	23°15'	15'	7
<i>Ipomoea brasiliensis</i> (L.) Sweet, Tropical Strand	23°30'	23°15'	15'	7
<i>Ipomoea stolonifera</i> (Cyr.) Gmel., Tropical Strand	23°30'	23°15'	15'	7
<i>Scaevola plumeri</i> (L.) Vahl, Tropical Strand	23°30'	23°15'	15'	7

These taxa are endemic to the Pacific Coast of North America and are restricted to maritime habitats. Their apparent inability to move inland limits them to coastal or oceanic migratory routes. Both *Atriplex barclayana* and *Astragalus magdalenae* have endemic maritime subspecies, but since other elements of the species occur inland they are treated in the Endemic Inland-Maritime group.

The relationships of the endemic strand flora appear to be complex. When classified on the basis of closest probable affinities the endemic species fall into four groups: 1) species with Arctic or Beringian affinities, *Polygonum paronychia*, *Tanacetum camphoratum*, *T. douglasii*; 2) species with affinities to inland taxa of mesic temperate areas, *Agrostis pallens*; 3) species with affinities to inland taxa of arid areas, *Abronia latifolia*, *A. maritima*, *Ambrosia chamissonis*, *Camissonia cheiranthifolia*; and 4) species whose affinities are not readily apparent, *Jouvea pilosa*, *Lathyrus littoralis*, *Suaeda californica*, *Poa douglasii*, *Chamaesyce leucophylla*.

Nine of the endemic species occur in the temperate region between 54° and 36°30'N latitude, with their ranges centering around 41°. Three species have arctic affinities, three have arid-inland affinities, while only *Agrostis pallens* shows affinities with the adjacent mesic inland flora. Of the remaining four endemic maritime species, only *Abronia maritima* shows possible arid-inland relationships. The affinities of the other three species are obscure.

V. Endemic Inland-Maritime: 6 species, 13 percent of the flora.

Taxa: *Atriplex barclayana*, *A. leucophylla*, *Arthrocnemum subterminale*, *Astragalus magdalenae*, *Frankenia palmeri*, *Lycium brevipes*.

Unlike the endemic maritime taxa, these species also occur in inland habitats. They are endemic, then, to western North America. *Astragalus magdalenae* and *Lycium brevipes* are found on gravelly or sandy areas inland; the other members of the group occur in saline or alkaline situations. In contrast to the maritime endemics that are predominately in the mesic latitudes, the inland-maritime endemics are found mainly in the arid regions between 32° and 24°N (*Atriplex leucophylla* forms the only exception, extending north to 41°).

Both *Astragalus magdalenae* and *Atriplex barclayana* have subspecies restricted to either maritime or inland areas, but there is no evidence of any morphological divergence between the inland and strand populations for the other four species in the endemic inland-maritime group.

There is a total of 19 endemic species on the Pacific Coast beaches accounting for 41 percent of the beach flora, which reflects the high degree of isolation of the Pacific Coast. Whether the inland-maritime species are paleoendemics having utilized overland migratory routes to reach the Pacific coast from other oceanic shores is not evident from the fossil record. Present day distributions and taxonomic affinities strongly suggest *in situ* evolution.

VI. Widespread Inland-Maritime: 3 species, 6 percent of the flora.

Taxa: *Allenrolfea occidentalis*, *Distichlis spicata*, *Heliotropium curassavicum*.

The three species included here are similar to those in the Temperate and Tropical Strand elements in that they occur on the beaches of more than one ocean or continent. However, their ability to occupy arid, saline or alkaline inland habitats provides them with migratory routes not open to species limited to the oceanic strand. In the *Distichlis spicata-stricta* complex, inland forms can be distinguished from coastal ones. If these forms represent ecotypes then one must allow for their multiple development or else assume that the migration routes for the coastal forms are limited to the oceanic strand. The former assumption could help explain the taxonomic difficulties found in the complex.

VII. Temperate Beach: 3 species, 6.5 percent of the flora.

Taxa: *Calystegia soldanella*, *Fragaria chiloensis*, *Mesembryanthemum chilense*.

As treated here the Temperate Beach element consists of species found on the beaches of more than one ocean or continent, but whose ranges do not extend inland or into arctic or tropical latitudes. The paucity of such taxa on the North American Pacific coast demonstrates its isolation from temperate oceanic migratory routes. How did these three species arrive?

Based on its fruit morphology *Fragaria chiloensis* is certainly an endozoochore rather than a hydrochore. Van der Pijl (1969) does not consider *Fragaria* as "typically ornithochorous" because its fruits possess an odor. However, given the disjunct occurrence of ssp. *pacifica* in temperate North and South America and Hawaii, bird dispersal seems reasonable.

Calystegia soldanella and *Mesembryanthemum chilense* appear to be the only Temperate Beach species for which widespread dispersal by ocean currents can be invoked, and the status of the latter as a native is open to question (see Moran, 1950). The disjunct occurrence of the two species in both the north and south hemispheres raises the possibility that, like *Cakile*, their present ranges may be the result of early introductions in ship ballast (Barbour and Rodman, 1970).

VIII. Tropical Beach: 5 species, 11 percent of the flora.

Taxa: *Ipomoea brasiliensis*, *I. stolonifera*, *Scaevola plumeri*, *Sesuvium portulacastrum*, *Sporobolus virginicus*.

Tropical Beach species are of relative minor importance in the area of discussion since they are limited to the tip of Baja California. Their migratory routes from continent to continent are essentially oceanic, distinguishing them from the Widespread Inland-Maritime species capable of utilizing overland routes.

IX. Introduced species: 4 species, 9 percent of the flora.

Taxa: *Ammophila arenaria*, *Cakile endentula*, *C. maritima*, *Mesembryanthemum edule*.

Introduced species, with the possible exception of *M. edule*, have become dominant elements in the beach vegetation over much of the temperate region. Given their importance in the vegetation and the fact that we are dealing here with ecological and not floristic units, we have included them in our analysis of the beach flora. For the same reasons Kohler (1970) found it necessary to utilize exotics in his classification of the Chilean strand vegetation.

As a group, the introduced species range from 60°N to 28°N, with the center of their distribution at 41° in the temperate region (54–36°N). The apparent lack of exotic taxa in the arctic and tropical regions considered in this paper could be due to the continuous nature of their respective migration routes, species capable of utilizing them have already attained their potential distributions.

The success of introduced taxa on the temperate Pacific coasts of both North and South America may be analogous to island situations, where incidence of new arrivals is too low to provide a closed community. As a result, competitive interaction is thought to be minimal. Consequently, introductions have proven highly successful—either by filling previously unfilled niches or by aggressively replacing indigenous species (Carlquist, 1965).

Construction of Eco-floristic Zones. The beach habitat along the Pacific Coast of North America is a classic example of a latitudinal gradient. Elevation is uniform, variety of aspect and substrate are limited, and the flora is relatively impoverished. Yet, an attempt to divide the coast into homogeneous zones along this gradient is difficult since the species tend to have overlapping ranges and rarely share both northern and southern limits. Further, there are no universally accepted criteria on which to base floristic regions. For example, floristic regions as defined by Stebbins and Major (1965) are based on degree of endemism, which is generally considered an indicator of isolation, age, and/or uniqueness of habitat. At the other extreme, Young (1971) ignored endemism entirely in dealing with the arctic flora and based his zones on coincidence of the northern limits of taxa.

In defining our eco-floristic zones, we have emphasized regions where abrupt and marked floristic changes occur. To locate such regions, the beach flora for each 30' of latitude was determined using the ranges given in Table 2. The assumption is made that a species' range is continuous between the extremes. The floras between adjacent 30' segments were then compared for similarity using Sorensen's coefficient of community (K; Sorensen, 1948).

$$K = \frac{2 \times \text{species in common, 30' segments A and B}}{\text{species in A} + \text{species in B}}$$

The resulting K values are shown in Table 3. The 30' segments generally show a high degree of similarity to adjacent segments; however, some segments do show an abrupt loss in similarity when compared to their adjacent segment(s).

The 30' segment having the lowest K value was selected as a provisional boundary segment (PBS) and each successive adjacent 30' segment to the south of the PBS was tested by similarity against it. Typically, K decreased gradually at a relatively uniform rate with increasing distance from the PBS. Once K dropped below 0.50 further testing of more distant segments was discontinued. The PBS and the adjacent series of continuous 30' segments to the south having $K > 0.50$ were considered a protozone.

TABLE 3. FREQUENCY OF OCCURRENCE OF K VALUES. An asterisk indicates less than five species in that segment's flora. The northern boundaries of the 30' segments are listed.

K	Number of occurrences	30' segment of occurrence
1.00	61	All segments not shown below.
0.98	3	53°, 40°30', 41°30'
0.97	3	50°, 48°30', 40°
0.96	3	36°, 35°, 34°30'
0.95	6	49°, 42°, 41°, 34°, 34°30', 30°
0.94	3	66°, 39°, 37°30'
0.93	1	25°30'
0.89	3	43°30', 31°, 29°30'
0.87	2	32°30', 28°30'
0.86	2	68°, 27°
0.83	1	36°30'
0.80	2	69°*, 28°
0.79	1	60°
0.77	1	24°30'
0.74	1	54°
0.67	2	24°*, 23°30'
0.62	1	32°

There is some empirical evidence that the 0.5 level of similarity marks the lower limit of homogeneity within important vegetational units. Both Sorensen (1948) in Denmark and Looman and Campbell (1960) in Saskatchewan found that stands within the same Braun-Blanquet association or subassociation shared K values of 0.5 or above. However, our values will not be strictly comparable, because those investigators compared complete species lists of plants, not just characteristic species, as we have done.

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The northern 30' segment adjacent to the original PBS was then utilized as a new PBS and successive adjacent northern segments tested against it for similarity until a northern protozone could be delimited.

A 30' segment showing the next lowest K value was then selected from the original list (Table 3) and the entire process repeated, forming two more protozones. Selection of new PBS's on the basis of their K value and subsequent protozone formation was continued until each 30' segment of the coast was included in at least one protozone. (Those 30' segments having four or fewer species in their flora were temporarily rejected as PBS choices. We found K to be unreliable when either A or B had less than five species.)

All 30' segments could be assigned to a protozone after utilizing the five lowest PBS's, i.e., 32°, 23°30', 54°, 24°30', and 60°N. However, several of these protozone boundaries were in latitudes of a very low rate of species change. The boundary at 41°N, for example (fig. 3), showed 30' segments just north and south to have K values of 0.95. Operationally, our method was to continue to select more PBS's until the protozone boundaries had a K value (adjacent 30' segments) lower than that for remaining PBS's in Table 3. It was necessary to select two more PBS's (28°, 36°30') and form four additional protozones before maximum cleavage between all protozones was achieved (fig. 3). From this, we made our final selection of appropriate boundaries and zones.

The following criteria were utilized in selecting these final boundaries: 1) the zones had to be discrete and not overlap; 2) all 30' segments had to be assigned to a zone; 3) abrupt changes in similarity were favored over gradual changes; and 4) a 30' segment had to have a K value of 0.50 or greater with both boundaries of its zone. The resulting classification is shown in Figure 4 and tables 4 and 5.

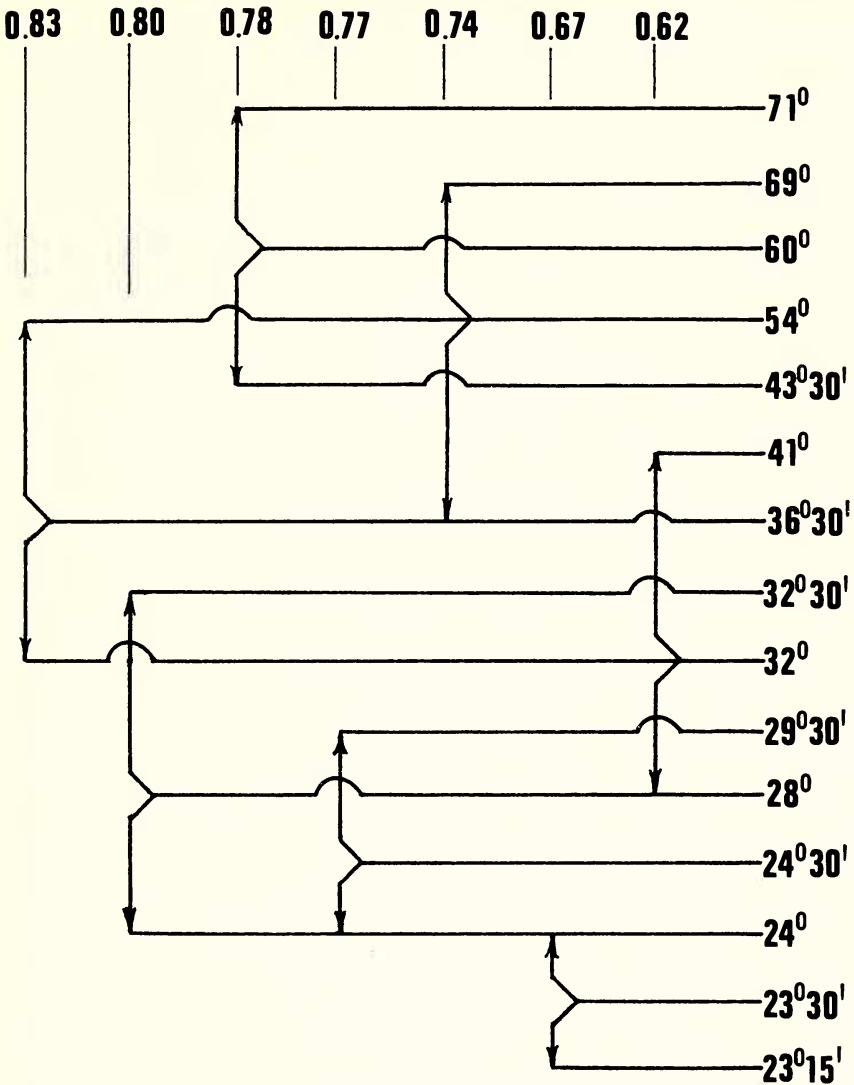


FIG. 3. Diagrammatic representation of the protozones and PBS's, from which the final, non-overlapping zones were drawn (Fig. 4). Figures on the extreme right are K values for the 30' segments just above and below the latitudes shown. The figures along the bottom indicate the K values of the seven PBS's used (e.g., 0.62 refers to the PBS at 32°N).

Discussion of the Zones. Species comprising beach vegetation in the Arctic zone are widespread strand plants with Circumarctic or Beringian-Eastern North America distributions. All of the species also occur in the Subarctic zone and most extend southward to the Temperate zone as well.

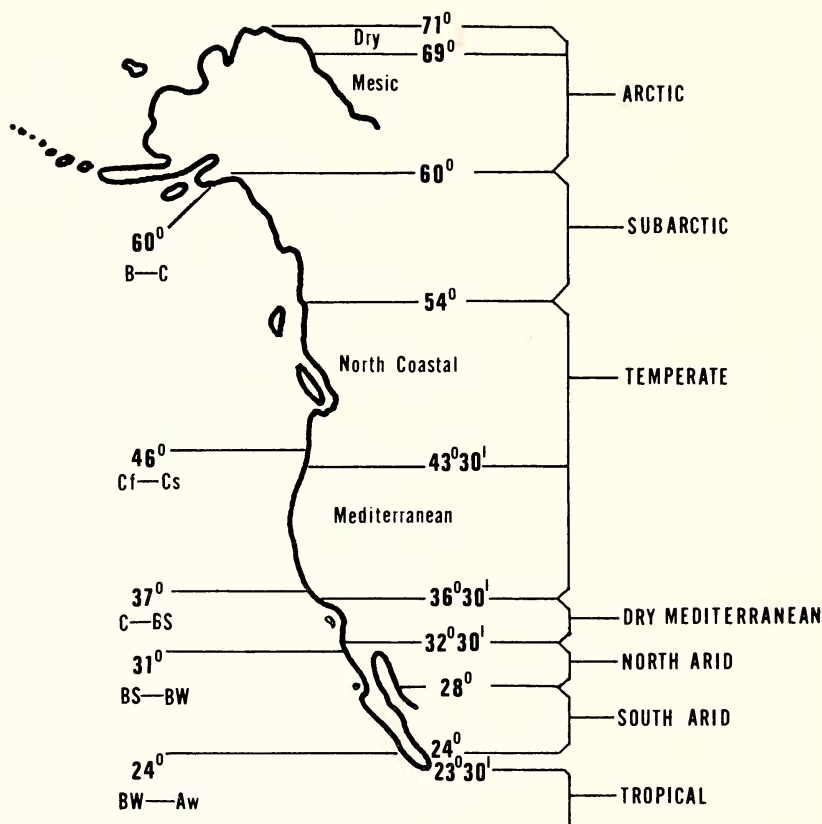


FIG. 4. Pacific coast eco-floristic zones and subzones and major climatic boundaries (Koeppen system).

The southward increase in the Arctic beach flora is a phenomenon of the arctic flora in general and can be correlated with increasing warmth, rainfall, or equability (Merriam, 1894; Nordenskjord and Meckling, 1928; Kimble and Good, 1955; Hopkins, 1959; Young, 1971). Young divided the arctic flora into four zones that he correlated with available summer warmth. The sub-boundary at 69°N between the Dry Arctic and the Mesic Arctic beach flora does appear to correspond to the boundary between Young's zones 2 and 3. Other than this one exception, the distributions of the Arctic and Subarctic beach taxa fail to coincide with Young's zonation. Young attributed this discrepancy in distribution between the beach species and the rest of the Arctic flora to the destructive action of pack ice and depression in summer warmth found in a strongly maritime environment.

The Subarctic zone is composed primarily of Arctic, Beringian-Eastern North American, and Beringian taxa that in a group continue to influence the beach flora south to 43°30'N—the southern limit of the

TABLE 4. COEFFICIENT OF SIMILARITY BETWEEN THE ECO-FLORISTIC ZONES AND SUBZONES. The number of species shared between two zones is given on the top line of a row and the K value for the two zones is given on the second line (e.g., zones 4 and 5 share 5 spp. and have a K value of 0.40).

	1a	1b	2	3a	3b	4	5	6	7
1a, Dry Arctic	4								
	1.00								
1b, Mesic Arctic	4	9							
	0.62	1.00							
2, Subarctic	4	9	14						
	0.44	0.79	1.00						
3a, North Coastal Temperate	4	9	12	23					
	0.30	0.56	0.70	1.00					
3b, Mediterranean Temperate	2	4	7	17	23				
	0.15	0.25	0.38	0.74	1.00				
4, Dry Mediterranean	0	0	2	7	12	13			
	-	-	0.15	0.39	0.67	1.00			
5, North Arid	0	0	0	2	4	5	12		
	-	-	-	0.11	0.23	0.40	1.00		
6, South Arid	0	0	0	0	1	2	6	9	
	-	-	-	-	0.06	0.18	0.57	1.00	
7, Tropical	0	0	0	0	0	0	1	3	8
	-	-	-	-	-	-	0.10	0.35	1.00

North Coastal Temperate subzone. While the floristic importance of this group is minimal below 43°30'N, *Elymus mollis* still continues to be an important dominant south to 36°30'N (Cooper, 1936).

Increase of the beach flora on the southern edge of the Alaskan peninsula coincides closely with the northern limits of Van Dyke's (1919, 1929) Vancouverian faunal area and with the boundary between Koepen's microthermal (D) and mesothermal (C) climate types. The criterion for separating the two climates is whether the mean temperature of the coldest month is above or below -3°C, which supposedly shows a rough correlation with the southern limits of frozen ground and snow cover lasting for a month or more (Trewartha, 1954). If one uses Ackerman's criterion of 0°C rather than -3°C for separating the C and D climates, then the southern limit of the D climate corresponds to the boundary between the Subarctic and Temperate beach zones at 54°N latitude. At any event, the close coincidence of the floristic boundaries with a change in severity of winter cold, appears to contradict the tenet that summer warmth alone is the major climatic factor controlling the northern limits of plant distribution in arctic-alpine areas (see, for example, Daubenmire, 1954).

The Temperate zone, covering 17°30' of latitude, is the largest of the floristic zones. It is characterized by a large endemic element and a high rate of species turnover between Arctic-Beringian species and endemic taxa (see fig. 2 and Table 5). Minor shifts occur in the flora between

TABLE 5. FREQUENCY OF OCCURRENCE OF DISTRIBUTION-TYPES IN THE ECO-FLORISTIC ZONES. Top line of each row gives the number of species of the distribution-type occurring in the zone and its percentage of the zone's flora. The second line of each row gives the percentage of the total number of species in the distribution-type which occur in the zone.

Zone or subzone (and total no. spp.)	Distribution types (and total number of species)								
	Circumarctic (5)	Beringian-E.N.A. (5)	Beringian (2)	Temperate Beach (3)	Introduced (4)	Maritime-Endemic (13)	Endemic Inland-Maritime (6)	Widespread Inland-Maritime (3)	Tropical Beach (5)
1a, Dry Arctic (4)	3;75	1;25							
1b, Mesic Arctic (9)	60	20							
	4;44	5;56							
2, Subarctic (14)	80	100							
	5;36	5;36	2;14	1; 7	1; 7				
	100	100	100	33	25				
3a, North Coastal Temperate (23)	5;22	4;17	2; 9	2; 9	3;13	7;30			
	100	80	100	67	75	56			
3b, Mediterranean Temperate (23)	1; 4	3;13	1; 4	3;13	4;17	9;39	1; 4	1; 4	
	20	60	50	100	100	69	17	33	
				3;23	4;31	4;31	1; 8	1; 8	
4, Dry Mediterranean (13)				100	100	31	17	33	
					1; 8	3;25	5;42	3;25	
					25	33	83	100	
5, North Arid (9)						1;11	4;44	2;22	2;22
6, South Arid (9)						11	67	67	40
7, Tropical (8)						2;25	2;25	0	4;50
						22	33	0	80

50° and 48°30'N where two endemic species (*Tanacetum douglasii*, *Polygonum paronychia*) reach their northern limits and two Arctic species (*Senecio pseudo-arnica*, *Ligusticum scoticum*) reach a southern limit. Replacement of Arctic-Subarctic elements by endemic species culminates at 43°30'N—the boundary between the North Coastal Temperate and Mediterranean Temperate subzones. While the boundary is not an abrupt one ($K = 0.89$ for 44°/43°30', Table 3), it does mark the northern and southern limits of significant influence by the Dry Mediterranean and Subarctic floras respectively. The Temperate Mediterranean subzone is characterized by a high incidence of maritime endemics (41 percent of the subzone's flora falls into this class, and 69 percent of all endemics occur in this subzone).

There is a gradual decline in summer precipitation southward in the Temperate zone with a major shift around 46°N where the climate changes from a Cf type, lacking a dry season, to a Cs type, having a summer drought. Accompanying the decline in uniformity of precipitation is an increase in temperature equability. The change in the climate type appears to have little effect floristically until 43°30'N.

The boundary between the two Temperate subzones at 43°30'N, near Coos Bay, Oregon, closely corresponds to Howell's (1957) northern boundary for the California floristic province. Inland, the Province's northern limits fall several degrees further south, along the Rogue River drainage. Stebbins and Major (1965) placed the coastal limit of the California floristic province at the mouth of the Rogue River in Oregon, approximately one degree south of Howell's line. Howell attributed the coastal extension of the California flora to “. . . the effect of higher summer temperatures modified by coastal fogs . . . [and to] . . . certain ancient rocks of the Klamath Mountain area”. He did not consider the possible roles of precipitation nor the modifying effect of the maritime climate on frost. It is difficult to ascertain the role of frost on the beach flora from available data. Barbour (1970c) found that the occurrence of frost was significantly less on the beach than in adjacent dunes. It is possible that species having a low frost tolerance could extend further northward in the beach habitat than in other maritime habitats.

Because of the open nature of the vegetation it can be argued that the high rate of species turnover is due solely to differences in tolerance to the abiotic environment. However, the beach may not be as open as it appears.

The beach is a permanently disturbed habitat, the flora of which consists of pioneer or colonizing species. Yet when the California beach flora is compared to the adjacent inland pioneer (weed) flora (as compiled by Robbins et al., 1970), there is a marked difference in the proportion of annual to perennial plants. Annuals comprise 54 percent of the weed flora, but they comprise only nine percent of the beach flora. The low percentage of annuals in the beach environment could be due to difficulties experienced in seedling establishment. Barbour's (1970c,

1972b) studies on the autecology of *Cakile maritima* and *C. edentula* indicate that difficulty in seedling establishment may be due to a limited number of suitable microsites on the beach. These species are short-lived, nearly annual plants whose dimorphic fruits allow for both amphicarp and hydrochory, which results in both extremely limited and widespread dispersal of diaspores. Barbour found nearly all *Cakile* seedlings to be located within a two meter radius of parent clumps. Thus, in behavior, *Cakile* is essentially a perennial in that once established it can maintain itself for a long period in a site. Further, he was able to attribute the replacement of *C. edentula* by *C. maritima* to the greater seed production of the latter, which increased its chances of attaining a suitable site.

Despite the high turnover rate in species, the number of species is fairly constant throughout the Temperate zone (Table 5). This uniformity in species number strongly suggests that there are a limited number of possible niches available on the beach and that we have species replacement within those finite niches in the Temperate zone. If this is true, then both the number of niches and micro-sites are limited and the chances of a seed attaining a favorable site for germination and growth is slight. As a result there is a strong selection for plants capable of retaining a site either by perennial growth or amphicarp and competition for a site is to be expected. Thus biotic interactions must be considered in "explaining" the distribution of beach species.

Between 37° and 36°30'N, a decrease in precipitation marks the change from a Mediterranean (Csb) to a semi-arid (BSskn) climate. Coincident with this change in climate, there used to be a change in the physiognomy of the vegetation and in beach topography. Prior to the introduction of *Ammophila*, *Elymus mollis* was a common dominant of the beaches north of 36°30' and formed a grassy foredune there, whereas both the grass and the foredune were lacking in the Dry Mediterranean zone below 36°30' (Cooper, 1936). Now, *Ammophila* has spread north and south of this line and has created its own unique foredune.

A marked reduction in the beach flora also coincides with the decreased rainfall between 37° and 36°30'N where five species reach their southern limits. Replacement is minimal: *Abronia maritima* is the only species to obtain its northern limits between 36° and 32°.

The sudden decline in the flora at 36°30'N could also be attributed to a lack of suitable habitats. The coast from 36°30'N south to 35°30'N consists primarily of cliffs and bluffs with the few beaches present being shallow and short. Payne et al. (1973) argue that the Monterey Peninsula with its "harsh aspect" has served as a barrier for *Ambrosia chamissonis*; the peninsula separates the populations south of Monterey from those to the north. *Cakile* species, whose diaspores can tolerate extended immersion in salt water (Barbour, 1972b), have migrated south of the Monterey Peninsula since their introduction into the San Francisco area (Barbour and Rodman, 1970), but to what extent *Ambrosia* fruits can

tolerate salt water or utilize ocean currents for dispersal is unknown. Occurrence of *Ambrosia* on isolated cove beaches in Northern California suggests that it is not dependent on a continuous beach or dune system for dispersal (personal observations).

The boundary at 36°30'N between Temperate Mediterranean and Dry Mediterranean zones corresponds closely to the faunal and floristic boundaries set by other workers. Van Dyke (1919, 1929) put the boundary between Vancouverian and Californian faunal areas near Pfeiffer Point, ca 36°15'N. Munz (1968) used Van Dyke's boundaries for his floristically oriented biotic provinces. Stebbins and Major (1965) considered 35°N to be an important floristic boundary. This agreement with our results is remarkable because they emphasized endemism in more inland maritime areas, whereas we emphasized sudden change in total species composition of an extreme maritime habitat.

In contrast to the high regional endemism of the adjacent inland flora, the Dry Mediterranean zone is anomalous, its only unique taxon is *Camissonia cheiranthifolia* ssp. *suffruticosa*. In lacking a unique floristic element and in its total number of species, the Dry Mediterranean zone is analogous to the Subarctic zone.

Within the Dry Mediterranean zone, rainfall declines from 426 mm at Morro Bay (35°20'N) to 334 mm at Avalon (33°21'N). An equal drop occurs between Avalon and San Diego (32°44'N). The flora also shows a decline: four species are lost between 35° and 32°30'N, while at 32°N a marked floristic shift occurs with three species reaching a southern limit and four a northern one ($K = 0.875$ for 32°30'–32°N, Table 3).

The sharp boundary formed at 32°N is to the north of any other floristic, climatic, or ecological boundary. Epling and Lewis (1942) considered the adjacent inland region to be the center of the Coastal Sage and Southern Coastal Chaparral communities. The southern boundary of both Howell's (1957) California flora province and Van Dyke's (1919, 1929) California faunal area is much further south (ca 30°30'N). Shreve (1936) considered the same boundary to be the northern limit for the Sonoran Desert in western Baja California. Johnson (1973) found that Baja California dune vegetation also showed a floristic shift near 30°30'N. North of this, *Abronia maritima* is the main beach species, with *Atriplex leucophylla*, *Suaeda californica*, and *Cakile maritima* its most common associates. South of this, *Cakile* and *Ambrosia chamissonis* drop out, and *Sesuvium verrucosum* becomes as prominent as *Abronia*. This major boundary (at 30°30'N) coincides roughly with the change from a semi-arid (BS) to an arid (BW) climate type near 30°N latitude.

A similar discrepancy appears to occur between the beach and inland flora in the boundary between the Northern and Southern Arid zones. At Punta Abreojos (26°30'N), the climate changes from a BWk to a BWb type due to the increasing mean annual temperature, which in

effect increases aridity. The coastal boundary between the Viscaïno and Magdalena deserts occurs approximately 20' to the south at Bahía San Juanico. Yet the shift from the Northern Arid to Southern Arid beach flora is found several degrees to the north at 28°30'N, near Punta Rosarita.

Likewise, the southern limits of the Southern Arid zone at 24°N near Puerto Magdalena is north of Shreve and Wiggins' (1964) southern limit for the Magdalena desert near Todos Santos at 23°30'N.

Thus, in the more xeric latitudes there is an obvious northward shift in the beach flora when compared to the adjacent inland flora. This suggests that, despite a cooler, maritime climate, the beach is a more extreme habitat than inland habitats in a regional Bs or BW climate.

The beaches here may also be more saline. The floras of the two Arid zones are dominated by Inland-Maritime species, the majority of which are found in saline or alkaline situations inland. In all, there is a total of nine Endemic and Widespread Inland-Maritime species, accounting for 64 percent of the Northern Arid zone's flora and 54 percent of the flora of the Southern Arid zone. Only two of these (*Heliotropium curassavicum*, *Atriplex leucophylla*) extend out of the Arid region. High incidence of otherwise inland halophytes and occurrence of typically salt marsh species such as *Distichlis spicata* and *Suaeda californica*, combined with the northward shift of the Arid zones' boundaries, suggests that the reduction in rainfall has reduced the rate of leaching and created a more saline soil than on beaches to the north.

We consider the region between 24° and 23°30'N to be an ecotone between the Southern Arid and Tropical zones. However, unlike most ecotones, the beach flora between Puerto Magdalena and Todos Santos is depauperate and shows a low degree of similarity to either adjacent zone. *Abronia* and *Sesuvium* continue as the dominant foredune builders until north of Todos Santos (23°30'N), where *Jouvea pilosa* and *Sporobolus virginicus*, two grasses, become dominant. Altogether at Todos Santos about ten beach and dune species make their first appearance and continue south around the cape. Many of the added taxa are pantropical (*Ipomoea*, *Scaevola*). Shreve and Wiggins (1964) and Johnson (1973) point out that this rapid coastal change is paralleled by inland change, from Magdalena desert (low scrub with *Larrea*, *Prosopis*, *Fouquieria*, *Encelia*) to cape thorn forest (woodland with *Lysiloma*, *Cercidium*, *Bursera*).

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LITERATURE CITED

- ACKERMAN, E. A. 1941. The Köppen classification of climates in North America. *Geogr. Rev.* (New York) 31:105-111.
- AMUNDSEN, C. C. and E. E. C. CLEBSCH. 1971. Dynamics of the terrestrial ecosystem vegetation of Amchitka Island, Alaska. *BioScience* 21:619-623.
- ARIAS, A. C. 1942. Mapa de las provincias climatológicas de la república Mexicana. Secretaría de Agricultura y Fomento, Inst. Geogr., Mexico.
- ARMSTRONG, R. H. 1971. Physical climatology of Amchitka Island, Alaska. *BioScience* 21:607-609.
- AXELROD, D. I. and H. P. BAILEY. 1969. Paleotemperature analysis of Tertiary floras. *Paleogeography* 6:163-195.
- BARBOUR, M. G. 1970a. The flora and plant communities of Bodega Head, California. *Madroño* 20:289-313.
- . 1970b. Germination and early growth of the strand plant *Cakile maritima*. *Bull. Torrey Bot. Club* 97:13-22.
- . 1970c. Seedling ecology of *Cakile maritima* along the California coast. *Bull. Torrey Bot. Club* 97:280-289.
- . 1970d. Is any angiosperm an obligate halophyte? *Amer. Midl. Naturalist* 84:105-120.
- . 1972a. Additions and corrections to the flora of Bodega Head, California. *Madroño* 21:446-448.
- . 1972b. Seedling establishment of *Cakile maritima* at Bodega Head, California. *Bull. Torrey Bot. Club* 99:11-16.
- , and J. E. Rodman. 1970. Saga of the west coast sea-rockets. *Cakile edentula* ssp. *californica* and *C. maritima*. *Rhodora* 72:370-386.
- , R. B. CRAIG, F. R. DRYSDALE, and M. T. GHISELIN. 1973. Bodega Head: coastal ecology. Univ. Calif. Press, Berkeley.
- BOWDEN, W. H. 1957. Cytotaxonomy of section *Psammelymus* of the genus *Elymus*. *Canad. J. Bot.* 35:951-993.
- BOYCE, S. G. 1954. The salt spray community. *Ecol. Monogr.* 24:29-67.
- BOUGHEY, A. S. 1968. A checklist of Orange County flowering plants. Museum of Systematic Biology, Univ. Calif., Irvine.
- BRANDEGEE, T. S. 1889. A collection of plants from Baja California. *Proc. Calif. Acad. Sci., Ser. 2*, 2:117-216.
- CARLQUIST, S. 1965. Island life. Natural History Press, Garden City, N.Y.
- CALDER, J. A. and R. L. TAYLOR. 1968. Flora of the Queen Charlotte Islands, part 1. Systematics of the vascular plants. Canada Dept. Agric. Monogr. No. 4, part 1, Ottawa.
- CHAPMAN, V. J. 1964. Coastal vegetation. MacMillan, N.Y.
- CLIMATE OF BRITISH COLUMBIA, report for 1944. 1945. Prov. of British Columbia Dept. of Agric., Victoria, B.C.
- CLIMATOLOGICAL DATA, United States by sections. 1968. U.S. Dept. Commerce, Washington, D.C.
- COOPER, W. S. 1936. The strand and dune flora of the Pacific Coast of North America: a geographic study, pp. 141-187. *In* T. H. Goodspeed (ed.). *Essays in geobotany*. Univ. Calif. Press, Berkeley.
- . 1958. Coastal sand dunes of Oregon and Washington. *Mem. Geol. Soc. Amer.* 72.
- . 1967. Coastal dunes of California. *Mem. Geol. Soc. Amer.* 104.
- DAUBENMIRE, R. 1954. Alpine timberlines in the Americas and their interpretation. *Butler Univ. Bot. Stud.* 11:119-136.
- EBER, L. E., J. F. T. SAUR, and O. E. SETTE. 1968. Monthly mean charts of sea surface temperature, North Pacific Ocean, 1949-62. U.S. Dept. Interior, Circ. 258, Washington, D.C.
- EPLING, C. and H. LEWIS. 1942. The centers of distribution of the chaparral and coastal sage associations. *Amer. Midl. Naturalist* 27:445-462.

- FERNALD, M. L. and C. A. WEATHERBY. 1916. The genus *Puccinellia* in Eastern North America. *Rhcdora* 18:1-23.
- FRANKLIN, J. F. and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. Government Printing Office, Washington, D.C.
- HALL, H. M. and F. E. CLEMENTS. 1923. *Atriplex*. Publ. Carnegie Inst. Wash. No. 326. Washington, D.C.
- HAMBIDGE, G. (ed.). 1941. Climate and man. Yearbook of Agriculture, U.S. Dept. Agric., Washington, D.C.
- HASTINGS, J. R. and R. R. HUMPHREY (eds.). 1969. Climatological data and statistics for Baja California. Technical reports on the meteorology and climatology of arid regions, No. 18. Univ. of Arizona Inst. Atmos. Physics. Tucson, Arizona.
- HERMANN, F. J. 1960. Vetches in the United States—native, naturalized, and cultivated. U.S.D.A. Agric. Handb. 168:1-84.
- HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, and J. W. THOMPSON. 1969. Vascular plants of the Pacific Northwest, 5 Vols. Univ. Wash. Press, Seattle.
- HIGGINS, E. G. 1956. Coastal plants of San Diego. San Diego Soc. Nat. Hist., San Diego, Calif.
- HOOVER, R. F. 1970. The vascular plants of San Luis Obispo County, California. Univ. Calif. Press, Berkeley.
- HOPKINS, D. M. 1959. Some characteristics of the climate in forest and tundra regions in Alaska. *Arctic* 12:215-220.
- HOWELL, J. T. 1957. The California flora and its province. *Leaflet W. Bot.* 8:133-138.
- . 1970. *Marin flora*, 2nd ed. with supplement. Univ. Calif. Press, Berkeley.
- HULTÉN, E. 1937. Flora of the Aleutian Islands. Bokforlags Aktiebolaget Thule, Stockholm.
- . 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press, Stanford, Calif.
- JOHNSON, A. F. 1973. A survey of the strand and dune vegetation along the Pacific coast of Baja California, Mexico. M.S. Thesis, Univ. Calif., Davis.
- JOHNSON, B. H. 1958. The botany of the California Academy of Science expedition to Baja California in 1941. *Wasmann J. Biol.* 16:217-318.
- JONES, G. N. 1936. A botanical survey of the Olympic Peninsula, Washington. Univ. Wash. Press, Seattle.
- KEARNEY, T. H. 1904. Are plants of sea beaches and dunes true halophytes? *Bot. Gaz. (Crawfordsville)* 37:424-436.
- KIMBLE, G. and D. GOOD. 1955. Geography of the Northlands. *Amer. Geogr. Soc. Special Publ.* 32.
- KNAPP, R. 1965. Die vegetation von Nord- und Mittleamerika. Gustav Fischer Verlag, Stuttgart, Germany.
- KOEPPEL, C. E. 1931. The Canadian climate. McNight and McNight, Bloomington, Ill.
- KOHLER, A. 1970. Geobotanische untersuchungen an Künen Chiles zwischen 27 und 42 Grad südl. Breite. *Bot. Jahrb. Syst.* 90:55-200.
- KUMLER, M. L. 1969. Plant succession on the sand dunes of the Oregon coast. *Ecology* 50:695-704.
- LEWIS, W. H. and R. L. OLIVER. 1965. Realignment of *Calystegia* and *Convolvulus* (Convolvulaceae). *Ann. Missouri Bot. Gard.* 52:217-222.
- LOOMAN, J. and J. B. CAMPBELL. 1960. Adaptation of Srensen's K (1948) for estimating unit affinities in prairie vegetation. *Ecology* 41:409-416.
- MACARTHUR, R. H. 1972. *Geographical ecology*. Harper and Row, N.Y.
- MACDONALD, K. B. and M. G. BARBOUR. 1974. Beach and salt marsh vegetation along the Pacific Coast, pp. 175-234. *In* R. J. Reimold and W. H. Queen (eds.). *Ecology of halophytes*. Academic Press, N.Y.
- MARTIN, E. V. and F. E. CLEMENTS. 1939. Adaptation and origin in the plant world. 1. Factors and functions in coastal dunes. Carnegie Inst. Wash., Washington, D.C.

- MERRIAM, C. H. 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Natl. Geogr. Mag.* 6:229-238.
- MORAN, R. 1950. *Mesembryanthemum* in California. *Madroño* 10:129-160.
- MUNZ, P. A. 1973. A California flora and supplement. Univ. Calif. Press, Berkeley.
- NELSON, E. W. 1922. Lower California and its natural resources. *Natl. Acad. Sci.*, Washington, D.C. (Reproduced in 1966 by Manessier Publishing Co., Riverside, Calif.)
- NORDENSKJOLD, O. and L. MECKLING. 1928. The geography of the polar regions. *Amer. Geogr. Soc. Special Publ. No. 8.*
- OOSTING, H. J. 1954. Ecological processes and vegetation of the maritime strand in the United States. *Bot. Rev. (Lancaster)* 20:226-262.
- , and W. D. BILLINGS. 1942. Factors affecting vegetational zonation on coastal dunes. *Ecology* 23:131-142.
- ORCUTT, C. R. 1885. Flora of southern and lower California. A checklist of the flowering plants and ferns. Privately published pamphlet, San Diego, Calif.
- PAYNE, W. W. 1964. A re-evaluation of the genus *Ambrosia* (Compositae). *J. Arnold Arbor* 45:401-430.
- , T. A. GEISSMAN, A. J. LUCAS, and T. SAITOH. 1973. Chemosystematics and taxonomy of *Ambrosia chamissonis*. *Biochem. Syst.* 1:21-33.
- PECK, M. E. 1961. A manual of the higher plants of Oregon, 2nd ed. Oregon State Univ. Press, Corvallis.
- PURER, E. A. 1934. Foliar differences in eight dune and chaparral species. *Ecology* 15:197-203.
- . 1963. Studies of certain coastal sand dune plants of southern California. *Ecol. Monogr.* 6:1-87.
- RANWELL, D. S. 1972. Ecology of salt marshes and sand dunes. Chapman and Hall, London.
- RAVEN, P. H. 1969. A revision of the genus *Camissonia* (Onagraceae). *Contr. U.S. Natl. Herb.* 37:161-396.
- ROBBINS, W. W., M. K. BELLUE, and W. S. BALL. 1970. Weeds of California. State Documents & Publications, Sacramento, Calif.
- RODMAN, J. E. 1974. Systematics and evolution of the genus *Cakile* (Cruciferae). *Contr. Gray Herb.* 205:1-146.
- SCHOFIELD, W. B. 1969. Phytogeography of northwestern North America: bryophytes and vascular plants. *Madroño* 20:155-207.
- ST. JOHN, H. 1970. Classification and distribution of the *Ipomoea pescaprae* group (Convolvulaceae). *Breite. Bot. Jahrb. Syst.* 89:563-583.
- SHREVE, F. 1936. The transition from desert to chaparral in Baja California. *Madroño* 3:257-264.
- , and I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran desert, in 2 vols. Stanford Univ. Press, Stanford, Calif.
- SMALL, J. K. 1895. A monograph of the North American species of the genus *Polygonum*. *Mem. Dept. Bot. Columbia Coll.* 1:1-183.
- SMITH, C. F. 1952. A flora of Santa Barbara. Santa Barbara Botanic Garden, Santa Barbara, Calif.
- SORENSEN, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Biol. Meddel. Kongel. Danske Vidensk. Selsk.* 5(4):1-34.
- STEBBINS, G. L. and J. MAJOR. 1965. Endemism and speciation in the California flora. *Ecol. Monogr.* 35:1-35.
- SWALLEN, J. R. 1944. The Alaskan species of *Puccinellia*. *J. Wash. Acad. Sci.* 34:16-24.
- THOMAS, J. H. 1961. Flora of the Santa Cruz Mountains of California. Stanford Univ. Press, Stanford, Calif.
- THORNE, R. F. 1967. A flora of Santa Catalina Island, California. *Aliso* 6:1-77.
- TILLET, S. S. 1967. The maritime species of *Abronia* (Nyctaginaceae). *Brittonia* 19:299-327.

- TREWARTHA, G. T. 1954. An introduction to climate, 3rd ed. McGraw-Hill, N.Y.
- VAN DER PIJL, L. 1969. Principles of dispersal in higher plants. Springer-Verlag, N.Y.
- VAN DYKE, E. C. 1919. The distribution of insects in western North America. *Ann. Entomol. Soc. Amer.* 12:1-12.
- . 1929. The influence which geographical distribution has on the production of the insect fauna of North America. 4th Internat'l. Congr. Entom. Proc. pp. 556-566.
- WIGGINS, I. L. and J. H. THOMAS. 1962. A flora of the Alaskan Arctic Slope. Univ. Toronto Press, Toronto, Canada.
- WILLIAMS, W. T. 1974. Species dynamism in the Pacific coastal strand community at Morro Bay, California. *Bull. Torrey Bot. Club* (in press).
- , and J. R. POTTER. 1972. The coastal strand community at Morro Bay State Park, California. *Bull. Torrey Bot. Club* 99:163-171.
- YOUNG, S. B. 1971. The vascular flora of St. Lawrence Island with special reference to floristic zonation in the Arctic regions. *Contr. Gray Herb.* 201:11-115.

VASCULAR PLANTS ON A SPRUCE BALD IN COLORADO

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At Boreas Pass, just below tree-line on the Continental Divide, Summit County, Colorado (39° 25' N, 105° 58' W; 3,609-3,657 m elevation), there is a 90-year-old spruce bald. This bald was formed primarily by clear cutting practices carried out by the Denver, South Park, and Pacific Railroad in its construction of a line over Boreas Pass in 1882 (*Montezuma Millrun*, 1882). Fire has been a secondary influence in forming the bald (Ubbelohde, 1965; E. J. Haley, pers. comm., 1972).

The summit of the pass and the slopes approaching the summit comprise the bald. The area as a whole provides a mosaic configuration of unaltered sites, severely altered sites, and sites of intermediate disturbance among which comparisons of environmental changes may be made. A study of these differences indicates that the major factor controlling vegetation is substrate instability (Olgeirson, 1972). This feature has also been described as a determining factor in arctic vegetation (Raup, 1951; Sigafos, 1952).

Maintenance of the bald is due to the unfavorable influence of a drastically altered environment on tree reestablishment (Stahelin, 1943; Billings and Mark, 1957; Billings, 1969; Olgeirson, 1972). Environmental changes have also created a marked reorientation in herbaceous plant communities. Functionally, this change is regressional, marked by a trend toward vegetation having a physiognomy like alpine fell-fields; floristically, there is a trend toward increased frequency of vascular plants usually associated with the alpine tundra (Billings, 1957, 1969; Weber and Willard, 1967).